

Morphology of the digestive system of *Volutomitra alaskana* Dall, 1902 (Gastropoda, Pectinibranchia, Volutomitridae), with notes on a possible mechanism of feeding

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The morphology of the anterior alimentary system of *Volutomitra alaskana* Dall is described. It agrees in most details with published accounts for four other species within Volutomitridae. All volutomitrids studied to date possess a cuticularized, funnel-shaped jaw, and a medially-furrowed chitinous shield ventral to the buccal mass. Within Neogastropoda, the presence of tubular jaw has previously been reported only in the Cancellarioidea. The chitinous shield appears to be unique to Volutomitridae. Based on the morphology of the jaw, chitinous shield and radula, we propose a mechanism for their function, and suggest that Volutomitridae are suctorial feeders. This hypothesis is supported by additional similarities between the mid-esophagus of Volutomitridae and Cancellarioidea, which are known to be suctorial feeders.

Морфология пищеварительной системы *Volutomitra alaskana* Dall, 1902 (Gastropoda, Pectinibranchia, Volutomitridae), с замечаниями о возможном механизме питания

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Описана морфология пищеварительной системы переднего отдела пищеварительной системы *Volutomitra alaskana* Dall. В целом она очень близка к таковой, описанной в литературе для 4 видов Volutomitridae. Все изученные к настоящему моменту волутомитриды имеют кутикулизованную воронковидную челюсть и медиально вогнутый хитиновый щиток, располагающийся вентрально от буккальной массы. Трубовидная челюсть у Neogastropoda ранее была найдена только у Cancellarioidea. Хитиновый щиток оказывается уникальным для Volutomitridae. На основании морфологии челюсти, щитка и радулы предполагается, что Volutomitridae являются сосущими. Эта гипотеза подтверждается дополнительными чертами сходства морфологии среднего пищевода у Volutomitridae и Cancellarioidea. Для последних было показано, что они сосут кровь рыб.

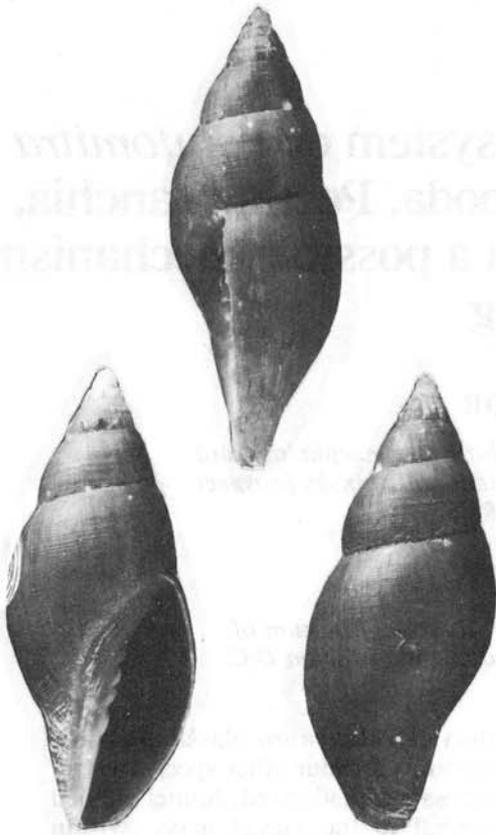


FIG 1. *Volutomitra alaskana* Dall, 1902. Apertural, lateral, and dorsal views of specimen from the Kurile Islands (ZMMU). Shell length — 28.5 mm.

РИС. 1. Раковина *Volutomitra alaskana* Dall, 1902. Курильские острова (ZMMU), высота раковины 28.5 мм.

INTRODUCTION

The Volutomitridae is a small family of rachi-glossan neogastropods of uncertain phylogenetic affinities. Early workers referred species now included in Volutomitridae to the family Mitridae [e.g. H. and A. Adams, 1853; Tryon, 1882] based on conchological similarity, or to the Volutidae [e.g. Gray, 1857; Fischer, 1887; Thiele, 1929; Wenz, 1943; Pilsbry, Olsson, 1954; Bayer, 1971] based on the resemblance of its radula to that of *Scaphella*. Cernohorsky [1970] accorded family level status to this group on the grounds that it has characters intermediate between the Volutidae and Mitridae, and most subsequent workers [e.g. Boss, 1982; Ponder, Waren, 1988] have followed this arrangement. Ponder [1972] provided detailed anatomical data for two New Zealand species (*Peculator hedleyi* (Murdoch, 1905) and *Microvoluta marginata* (Hutton, 1885)) and tabulated anatomical differences between the families Volutomitridae, Mitridae and Vexillidae. In a later work, Ponder [1973: 331] suggested that Volutomitridae may be a sister group of Marginellidae and listed

several shared anatomical features.

Cernohorsky [1970] monographed the family Volutomitridae, basing his classification almost exclusively on shell characters. Bayer [1971] described two additional species of *Volutomitra* from the southern Caribbean, while Arnaud and van Mol [1979] provided detailed descriptions of the anterior alimentary systems of two species from the Kerguelen Islands. Other than these papers, there has been little new information on this family. Virtually nothing is known of its diet or ecology.

We recently had the opportunity to study several preserved specimens of *Volutomitra alaskana* Dall, 1902 from the collections of the Zoological Institute of the Russian Academy of Sciences, St.Petersburg (ZIN) and the Zoological Museum of Moscow University (ZMMU). In this paper, we call attention to structures in the foregut of *V. alaskana* that have not previously been recognized in this family. We speculate as to the homologies of these structures, and the diet and feeding mechanisms of this species.

MATERIALS AND METHODS

Several specimens of both sexes (itemized below) were dissected. Portions of the anterior alimentary system of two specimens were embedded in paraffin, sectioned at 8 μ m, and stained with Masson's triple stain. The proboscis of one specimen was dissected out, its integument removed to expose the jaw, chitinous shield and buccal mass, and critical-point dried. The proboscis of an additional specimen was treated with warm 10% KOH until only the jaws, chitinous shield and radular ribbon remained. These structures were rinsed, air-dried and, together with the critical point dried proboscis tip, coated with carbon and gold-palladium, and examined using a Hitachi S-270 Scanning Electron Microscope.

Material examined: R/V "Academic Oparin", 2-nd cruise, sta. 93, south-eastern Kamchatka, 156°55.9'E, 50°26.1'N, depth 132 m, 15.08.1986 (1 specimen dissected, proboscis sectioned) (ZIN); R/V "Poseidon", sta. 83, Okhotsk Sea, Sakhalin Island, Elizaveta Cape, depth 110 m, 20.07.1978 (1 specimen sectioned) (ZIN); Kurile Islands, (radula, jaw, chitinous shield extracted) (ZMMU); R/V "Academic Oparin", 2-nd cruise, sta. 83, south-eastern Kamchatka, 157°03.7'E, 50°30.7'N, depth 130 m, (proboscis tip flayed, critical-point dried) (USNM).

An additional 20 specimens were examined for the presence of the operculum.

RESULTS

Morphology of the anterior alimentary system: The retracted proboscis (Fig. 4 A,B, pr)

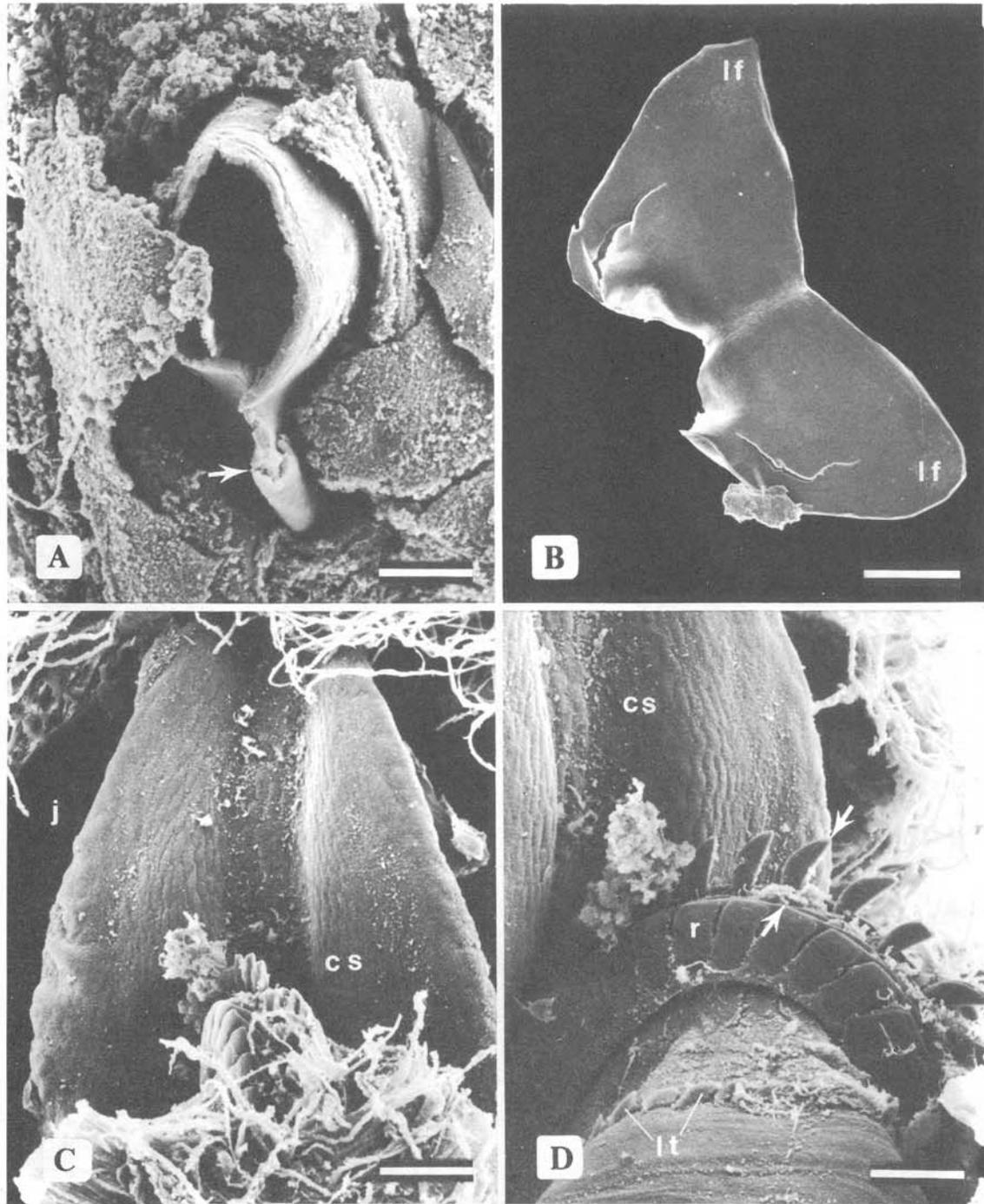


FIG. 2. Jaw and chitinous shield of *Volutomitra alaskana*.

A — Distal tip of jaw [critical-point dried], exposed by removing proboscis integument. Arrow indicates region of ventral overlap. Scale bar = $30\ \mu\text{m}$. B — Inner surface of unfolded jaw [air-dried]. Anterior to left of photo. Scale bar = $125\ \mu\text{m}$. C — Dorsal view of chitinous shield [critical-point dried]. Anterior at top of photograph. Scale bar = $35\ \mu\text{m}$. D — Lateral view of anterior tip of buccal mass [critical-point dried], illustrating relative positions of rachidian teeth, lateral teeth and chitinous shield. Cutting edge of rachidian tooth delimited by arrows. Scale bar = $25\ \mu\text{m}$.
 cs — chitinous shield; j — jaw; lf — lateral flaps; lt — lateral teeth of radula; r — rachidian teeth of radula.

РИС. 2. Челюсть и хитиновый щиток *Volutomitra alaskana*.

A — вершина челюсти [высушена при критической точке], покровы хобота удалены. Стрелкой обозначено место налегания боковых лопастей челюсти друг на друга. Масштабная линия = $30\ \mu\text{m}$. B — внутренняя поверхность расправленной челюсти [высушена на воздухе]. Передняя поверхность слева. Масштабная линия = $125\ \mu\text{m}$. C — дорсальный вид хитинового щитка [высушен при критической точке]. Передняя часть сверху. Масштабная линия = $35\ \mu\text{m}$. D — передний конец буккальной массы сбоку [высушена при критической точке], видно относительное расположение центральных и латеральных зубов и хитинового щитка. Режущий край центрального зуба обозначен стрелками. Масштабная линия = $25\ \mu\text{m}$.
 cs — хитиновый щиток; j — челюсть; lf — боковые лопасти челюсти; lt — латеральные зубы радулы; r — центральный зуб радулы.

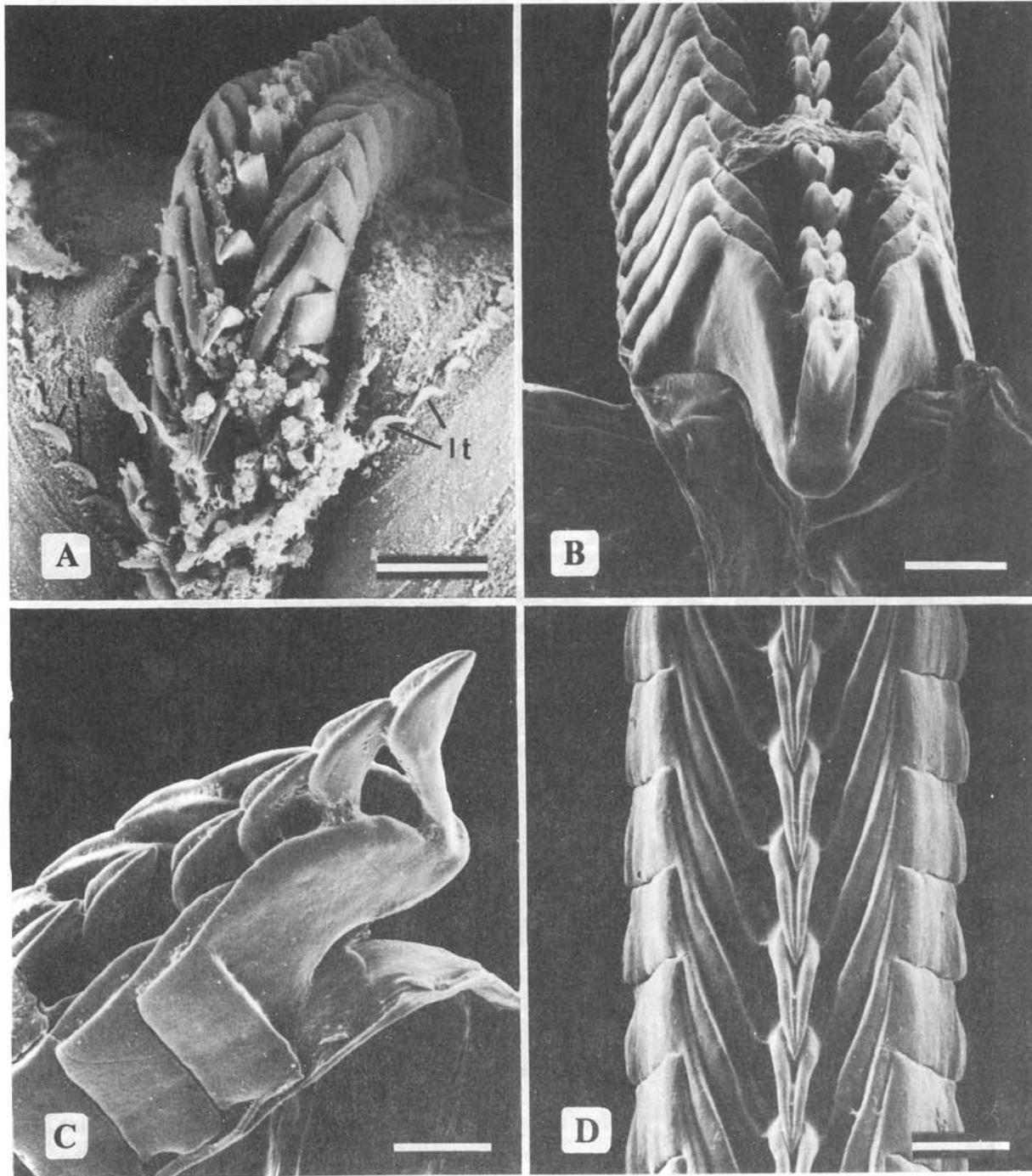


FIG. 3. A — Dorsal view of anterior tip of buccal mass [critical-point dried] of *Volutomitra alaskana*, illustrating relative position of rachidian and lateral teeth. Scale bar = 25 μm . B-D — Rachidian teeth of *Volutomitra alaskana*. Posterior (B), lateral (C), and dorsal (D) views. Scale bars = 30 μm .

РИС. 3. А — передняя часть буккальной массы *Volutomitra alaskana* с дорсальной стороны [высушена при критической точке]. Видно относительное положение центрального и латеральных зубов радулы. Масштабная линия = 23 μm . В-D — центральный зуб радулы *Volutomitra alaskana*. Вид сзади (В), сбоку (С), с дорсальной стороны (D). Масштабные линии = 30 μm .

is short and thick, tapering anteriorly toward a small, vertical, slit-like mouth. Large proboscis retractor muscles (Fig. 4B, prm) extend between the ventral side of the proboscis sheath and the columellar muscle in the posterior part of the

cephalic haemocoel. The proboscis is lined with tall, ciliated epithelium. The thick proboscis wall (Fig. 5A, prw) is composed of a thin outer layer of circular muscle, a thin intermediate layer of longitudinal muscle fibers, a thick inner layer of

loose circular muscle penetrated by numerous longitudinal and oblique muscle fibers, and an innermost layer of longitudinal muscles arranged in bundles. The anterior surface of the buccal cavity is lined by a cuticularized jaw. The left and right margins of the jaw overlap ventrally (Fig. 2A, arrow), forming an anteriorly-tapering, funnel-shaped enrolled tube that can be protruded through the mouth. The posteriorly directed lateral flaps of the jaw (Fig. 2B, lf) flank the juncture of the broad muscular esophagus (Fig. 5A, e) and the narrower buccal pouch (Figs. 4A, bp), which contains the buccal mass. The buccal mass is thin and elongate, extending beyond the posterior margin of the retracted proboscis and completely containing the radular sac.

The radula is long (≈ 4.3 mm), narrow (≈ 130 μm) and triserial, containing about 450 rows of teeth ($n = 1$). Each row contains a large rachidian tooth flanked by minute lateral teeth. The rachidian tooth (Fig. 2) has a complex form with a single, long, median cusp oriented nearly perpendicularly to the V-shaped and laterally buttressed basal plate. This cusp broadens distally to form a posteriorly pointing, V-shaped cutting edge. Lateral teeth (Figs. 2D, 3A, lt) appear to be composed of small (≈ 12 μm), posteriorly concave basal plates that lack projecting cusps. The odontophore is composed of a pair of short cartilages that do not fuse at their anterior ends (Fig. 5B, src). These odontophoral cartilages comprise about $\frac{2}{3}$ of the length of the retracted proboscis, and are attached along their posterior part to a muscular rod formed of longitudinal fibers. This rod extends well beyond the end of the proboscis (Fig. 4A, mr) and is connected by the short odontophoral retractor muscle (Fig. 4A, orm) to the esophagus near the nerve ring (Fig. 4A, nr).

A long (≈ 1.1 mm) chitinous shield (Fig. 5, cs) lines the ventral surface of the buccal pouch, which extends far beyond the anteriormost limit of the radula and is nearly long as the buccal mass. The anterior end of this shield, which has the form of a shallow gutter, is tapered and projects beyond the buccal mass into the buccal cavity enclosed by the jaw (Fig. 2 C,D). Longitudinal sections of the proboscis reveal that this chitinous shield originates from the cuticular lining of the sublingual pouch (Fig. 5, sp).

A small, unpaired accessory salivary gland, which is completely contained within the retracted proboscis, runs medially beneath the sublingual pouch and opens into the buccal cavity beneath the chitinous shield by very narrow duct (about 15 μm in diameter) (Fig. 5, dasg).

The morphology of the esophagus is very similar to that described for other species of Volutomitridae [e.g. *Peculator hedleyi* (Murdoch, 1905), see Ponder, 1972]. That portion of the anterior esophagus lying within the proboscis is broad and highly muscular, its thick walls lined with tall epithelial cells that bear long cilia.

Beneath this epithelium there is a thin layer of longitudinal muscle fibers and a thick layer of circular muscle penetrated by few longitudinal fibers. The outer part of the esophagus is formed by groups of circular muscles, connected to the proboscis wall by radial muscle fibers. After leaving the proboscis, the esophagus becomes narrower and has highly muscular walls composed of circular muscle. The ventral channel (Fig. 4C, vc) is lined with non-ciliated cuboidal epithelium in this region of the esophagus. Within the cephalic hemocoel, the esophagus is extremely long (while completely extended esophagus length $>$ shell length) and highly convoluted (Figs. 4 A,B), with adjacent loops connected to each other by muscle fibers to form a permanently rigid structure. The paired salivary glands (Fig. 4A, sg) flank the mid-esophagus just behind the small valve of Leiblein situated far anterior of the nerve ring (Fig. 4A, vL). Ducts from the salivary glands run laterally alongside the valve of Leiblein, and become embedded in the walls of the esophagus anterior to it (Fig. 4 C-F, dsg).

Torsion occurs in the posterior portion of the valve of Leiblein. In the anterior part of the valve, the ventral groove, which is continuous with the ventral channel of the esophagus, is situated ventrally, and is flanked by two zones of longitudinal muscles (Fig. 4D, lm). These zones of longitudinal muscles run the entire length of the valve. The folds of the epithelium become progressively higher, occupying nearly the entire lumen of the valve. These folds have cells with very long cilia that form a cone-like valve that runs nearly the entire length of the valve of Leiblein (Fig. 4 E-G, cv). Posteriorly, the paired zones of pale-staining mucous cells (Fig. 4E, mc) appear at both sides of the longitudinal muscles zones. Small supportive cells with very long cilia are situated between very tall cells with oval basal nuclei. Within a short span of the valve of Leiblein, the mucous cells (Fig. 4E, mc) are shifted to the dorsal side by zones of "squamous" cells (Fig. 4E-G, sc) with intensively staining granulated cytoplasm and moderately long cilia. These cells entirely replace the mucous cells. The clockwise rotation of the primary ventral channel is observed in this part of the valve, indicating the site of torsion. In all, the channel rotates about 70° .

Posterior to the valve of Leiblein, the esophagus widens and forms several loops prior to passing through the circumesophageal nervous ring (Fig. 4A, nr). Posterior to the nerve ring, the esophagus becomes greatly convoluted and has thick muscular walls. The posteriormost region of the mid-esophagus has extremely thick walls formed of circular muscles that greatly reduce its inner diameter (Fig. 4H). In this region, the short, narrow gland of Leiblein (Figs. 4 A,H, gL) joins the muscular esophagus. Posterior to this juncture, the esophagus becomes much narrower,

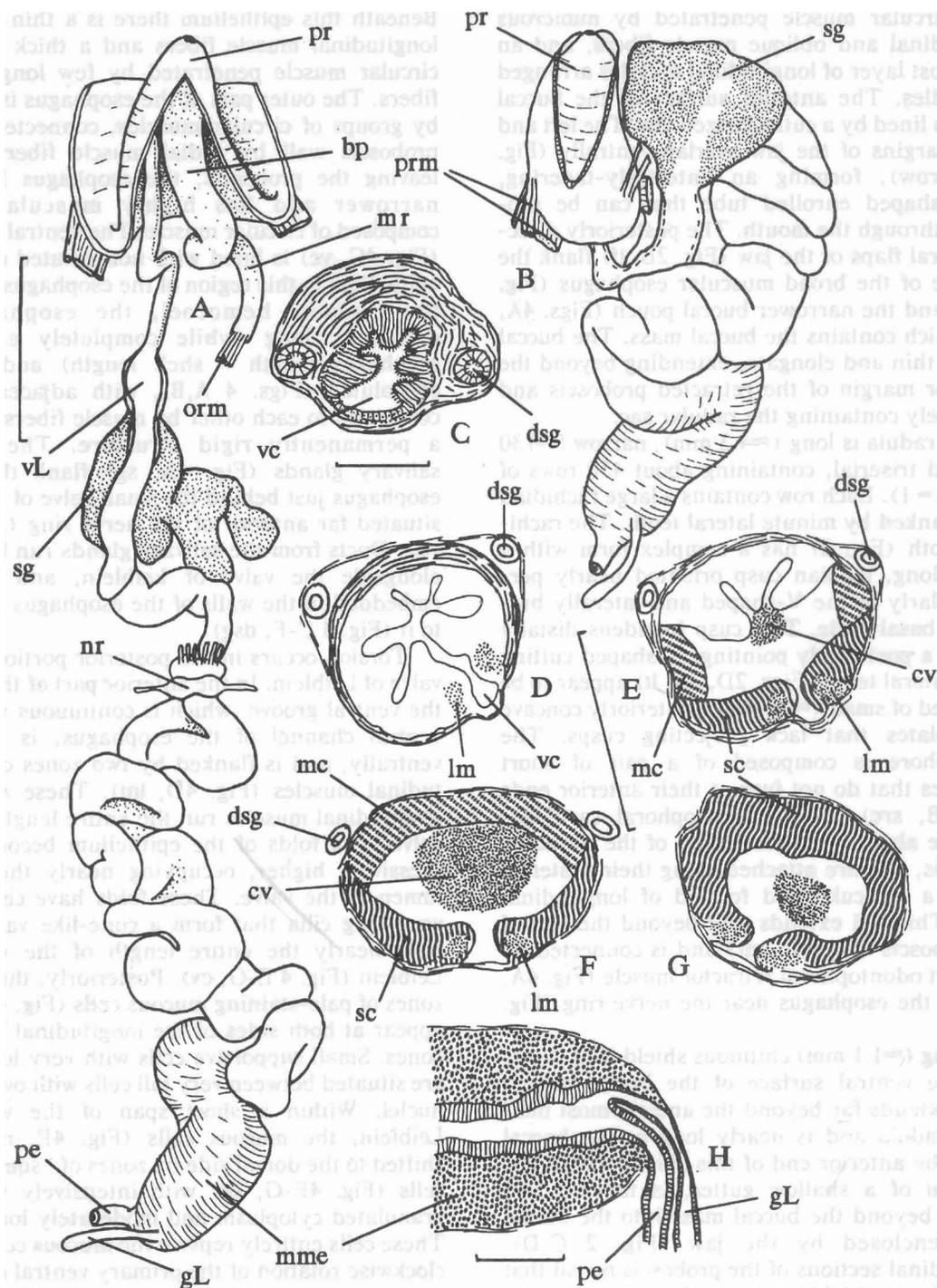


FIG. 4. Morphology of the anterior alimentary system of *Volutomitra alaskana* Dall. A — Organs of the cephalic haemocoel (scale bar = 0.5 mm); B — Organs of the cephalic haemocoel, partially extended (in the same scale as A); C — Transverse section through anterior esophagus (scale bar = 0.1 mm); D-G — Transverse sections through valve of Leiblein from anterior (D) to posterior (G) (scale bar = 0.5 mm); H — Longitudinal section through posterior end of the muscular mid-esophagus (scale bar = 0.5 mm). Abbreviations: bp — buccal pouch; cv — cone valve of cilia; dsG — duct of salivary gland; gL — gland of Leiblein; lm — longitudinal muscles; mc — mucus cells; mme — muscular part of mid-esophagus; mr — muscular rod; nr — circum-esophageal nerve ring; orm — odontophore retractor muscle; pe — posterior esophagus; pr — proboscis; prm — proboscis retractor muscles; sc — “squamous” cells; sg — salivary gland; vc — ventral channel; vL — valve of Leiblein.

РИС. 4. Морфология переднего отдела пищеварительной системы *Volutomitra alaskana* Dall. А — органы туловищного гемоцеля (масштабная линия = 0.5 мм); В — частично расправленные органы туловищного гемоцеля (в том же масштабе, как А); С — поперечный срез переднего пищевода (масштабная линия = 0.1 мм); D-G — поперечные срезы через клапан Лейблейна спереди (D) назад (G) (масштабная линия = 0.5 мм); H — продольный срез через задний конец мускулистой части пищевода (масштабная линия = 0.5 мм). Сокоращения: bp — буккальная масса; cv — конусовидный клапан из ресничек; dsG — проток слюнной железы; gL — железа Лейблейна; lm — зона продольных мускульных волокон; mc — слизистые клетки; mme — мускулистая часть среднего пищевода; mr — мускульный стебелек; nr — окологлоточное нервное кольцо; orm — ретрактор одонтофора; pe — задний пищевод; pr — хобот; prm — ретракторы хобота; sc — “чешуйчатые” клетки; sg — слюнная железа; vc — вентральный канал; vL — железа Лейблейна.

and less muscular (Figs. 4 A,H, pe), and leaves the cephalic hemocoel to join the stomach.

DISCUSSION

The morphology of the foregut of *Volutomitra alaskana* agrees in most regards with those of *Peculator hedleyi* and *Microvoluta marginata* (Hutton, 1885) [both described by Ponder, 1972] as well as with *Volutomitra curta* (Strebel, 1908) and *Volutomitra fragillima* (Watson, 1882) [described by Arnaud and van Mol, 1979]. The presence of long cilia in the valve of Leiblein, considered a primitive condition by Arnaud and van Mol [1979: 29], appears only in *V. alaskana* and *V. fragillima*, suggesting that *V. curta* may not be congeneric with these two species.

Ponder [1972: 324] reported the buccal walls of *Peculator hedleyi* to be "covered with a thin chitinous layer" and noted [1972: 330] a "weakly cuticulate oral invagination" in *Microvoluta australis*, but did not identify these structures as jaws. Arnaud and van Mol [1979: 29] report jaws to occur in *V. fragillima*, but do not mention them in their description of *V. curta*. These authors also confirm the presence of the chitinous shield in the volutomitrid species they studied, referring to it as a chitinous shield or plate [Arnaud and van Mol, 1979: 26, 29] or as a thick cuticular plate [Ponder, 1972: 324].

Although Carriker [1943] and Wu [1965] have reported a median dorsal sclerite in certain Muricidae, the presence of a tubular jaw within the order Neogastropoda has previously been reported only in the Cancellarioidea. The jaw of Volutomitridae, which apparently occur in all members of the family, bear considerable similarity to those of Cancellarioidea, especially of members of the subfamily Admetinae [see Oliver, 1982: fig. 4; Harasewych, Petit, 1986: fig. 6]. The jaw of Cancellarioidea [e.g. Petit, Harasewych, 1986: figs. 9,10] also overlap ventrally, but differs in having a long, tubular portion anteriorly, and in having the lateral flaps greatly expanded to envelope the buccal musculature, and radula-supporting cuticle [Harasewych, Petit, 1982, 1984, 1986]. The chitinous shield appears to be ubiquitous within and unique to the Volutomitridae.

Other than the suggestion that Volutomitridae "scrape particles of flesh or may even feed on body fluids which are sucked into the proboscis by the powerful buccal walls" [Ponder, 1972: 338], nothing is known of the diet or feeding of this family. No identifiable material was found in the foregut of the specimens of *V. alaskana* examined in this study, nor are we aware of any such reports for other species of Volutomitridae.

Data on the morphology of the jaw, chitinous shield and radula presented in this paper lead us to propose the following model for their function during feeding. The tip of the jaw is protruded

through the mouth and placed against the prey. With the protraction of the buccal mass, the chitinous shield slides forward along the ventral floor of the jaw, its tapered tip lodging near the aperture, or perhaps protruding no more than a few μm beyond it. As the aperture of the jaws and the rachidian teeth are approximately 40 μm wide, while the gutter of the chitinous shield is slightly narrower, we surmise that the function of this shield is to provide a gutter or groove through which the cusps of the rachidian teeth can move unimpeded prior to making contact with the prey. The lateral teeth cannot be protruded through the jaw aperture, but serve to maintain the alignment between the rachidian teeth and the gutter of the chitinous shield. As the individual rachidian cusps are protruded and make contact with their prey, they first pierce, then draw the integument toward the broader bases of the teeth, and finally cut through the integument prior to re-entering the aperture of the jaws. The overall effect is to slash or make incisions in the prey. Although the mechanism of radular action is analogous to that of a chain-saw, the depth of penetration is limited to the length of the median cusps above the rachidian bases (distance between the arrows in Fig. 2D), approximately 20-25 μm .

The minute oral aperture, small size of the radula, as well as radular morphology preclude ingestion of all but the smallest particles of solid food, and suggest that volutomitrids are fluid feeders.

It is interesting to note that Cancellarioidea, the only other Neogastropods to have tubular jaw, were inferred to be suctorial fluid feeders [Harasewych and Petit, 1982, 1984, 1986; Petit and Harasewych, 1986]. Subsequently, *Cancellaria cooperii* Gabb, 1865, was documented as feeding on the blood of the Pacific electric ray *Torpedo californica* Ayres [O'Sullivan et. al., 1987]. Suctorial feeding, also on the blood of fish, has recently been documented for two genera within the Marginellidae [Bouchet, 1989], a family considered to be closely related to Volutomitridae [Ponder, 1973].

Other features of the anterior alimentary system of Volutomitridae that are consistent with the hypothesis of suctorial feeding include: (1) the anterior migration of the valve of Leiblein, which has the effect of reducing the volume of food in the anterior esophagus, thereby enhancing interaction with salivary secretions and minimizing backflow of fluids posterior to it; (2) a simplified, elongated, and convoluted mid-esophagus where enzymatic digestion may take place; and (3) a greatly reduced gland of Leiblein. In cancellarioideans, the valve of Leiblein is situated near the rear of the buccal mass, the mid-esophagus is long, narrow and convoluted, and the gland of Leiblein is absent.

The prediction of suctorial feeding in Volutomitridae awaits empirical observation. However,

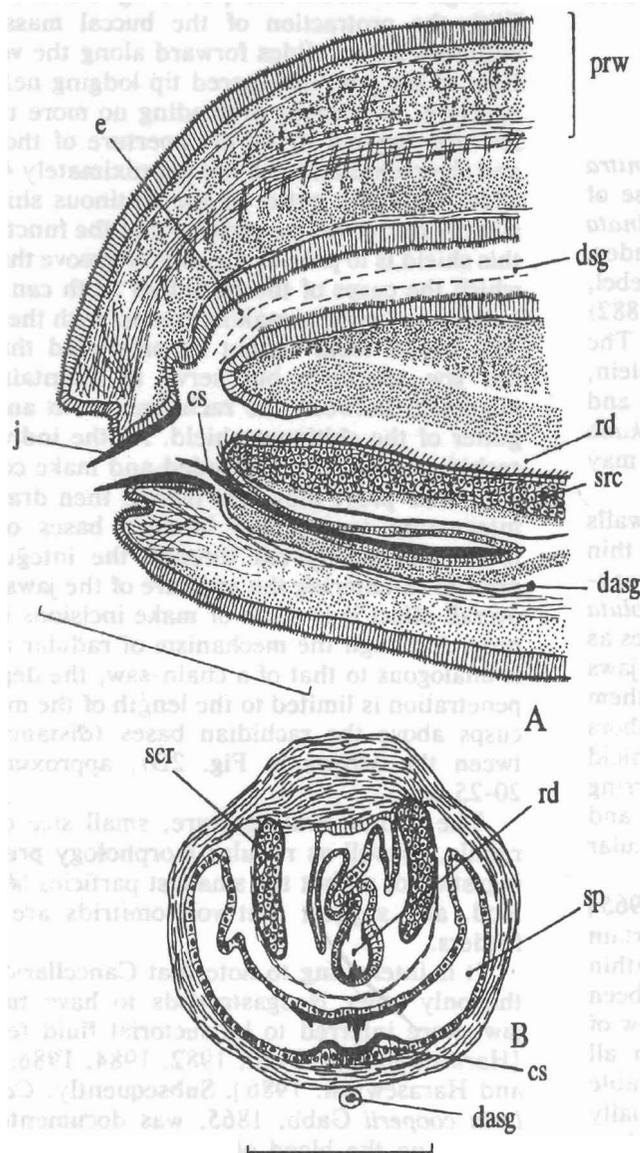


FIG. 5. Longitudinal section through the anterior portion of the proboscis (A, scale bar = 1 mm) and transverse sections through the anterior part of the odontophore (B, scale bar = 0.25 mm) of *Volutomitra alaskana*.

Position of the duct of the salivary gland passing in the esophageal wall is indicated by interrupted line.

Abbreviations: cs — chitinous shield; dasg — duct of accessory salivary gland; dsg — duct of salivary gland; j — jaw; e — esophagus; prw — proboscis wall; rd — radular diverticulum; src — subradular cartilages; sp — sublingual pouch.

Рис. 5. Продольный срез через переднюю часть хобота (А, масштабная линия = 1 мм) и поперечный срез через переднюю часть одонтофора (В, масштабная линия = 0.25 мм) *Volutomitra alaskana*.

Проток слюнной железы, проходящий в стенке пищевода показан пунктирной линией.

Сокращения: cs — хитиновый щиток; dasg — проток дополнительной слюнной железы; dsg — проток слюнной железы; e — пищевод; j — челюсть; prw — стенка хобота; rd — радулярное влагалище; src — субрадулярные хрящи; sp — субрадулярный карман.

the striking similarities of the anterior alimentary systems of *Volutomitridae* and *Cancellarioidea* either represent an extraordinary example of morphological convergence, or indicate that a reassessment of the systematic position and rank of these higher taxa is warranted.

Parenthetically, we note the absence of an operculum in all 24 of the specimens of *Volutomitra alaskana* that we were able to examine. This suggests that the operculum of this species figured by Cernohorsky [1970: pl. 13, figs. 3,4) was either anomalous, or misattributed. Larval shells 2.5 mm in length that were removed from egg capsules do have small transparent opercula

(Y.K., unpublished observations), which are normally lost during the course of development.

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